

## RESEARCH ARTICLE

# Protective buttressing of the human fist and the evolution of hominin hands

Michael H. Morgan<sup>1</sup> and David R. Carrier<sup>2,\*</sup>

<sup>1</sup>The University of Utah School of Medicine, 30 N. 1900 E., Salt Lake City, UT 84132, USA and <sup>2</sup>Department of Biology, University of Utah, 257 S. 1400 E., Salt Lake City, UT 84112, USA

\*Author for correspondence (carrier@biology.utah.edu)

### SUMMARY

The derived proportions of the human hand may provide supportive buttressing that protects the hand from injury when striking with a fist. Flexion of digits 2–5 results in buttressing of the pads of the distal phalanges against the central palm and the palmar pads of the proximal phalanges. Additionally, adduction of the thenar eminence to abut the dorsal surface of the distal phalanges of digits 2 and 3 locks these digits into a solid configuration that may allow a transfer of energy through the thenar eminence to the wrist. To test the hypothesis of a performance advantage, we measured: (1) the forces and rate of change of acceleration (jerk) from maximum effort strikes of subjects striking with a fist and an open hand; (2) the static stiffness of the second metacarpophalangeal (MCP) joint in buttressed and unbuttressed fist postures; and (3) static force transfer from digits 2 and 3 to digit 1 also in buttressed and unbuttressed fist postures. We found that peak forces, force impulses and peak jerk did not differ between the closed fist and open palm strikes. However, the structure of the human fist provides buttressing that increases the stiffness of the second MCP joint by fourfold and, as a result of force transfer through the thenar eminence, more than doubles the ability of the proximal phalanges to transmit ‘punching’ force. Thus, the proportions of the human hand provide a performance advantage when striking with a fist. We propose that the derived proportions of hominin hands reflect, in part, sexual selection to improve fighting performance.

Key words: male–male competition, fighting, great ape, Hominidae.

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### INTRODUCTION

The shape of our hand distinguishes us from the other apes (Fig. 1). In comparison to other apes, humans have short palms and fingers (i.e. digits 2–5), but long, strong and mobile thumbs (i.e. digit 1) (Schultz, 1930; Ashley-Montagu, 1931; Midlo, 1934; Jouffroy et al., 1991; Christel, 1993; Watkins et al., 1993; Susman, 1994). These proportions, combined with the mobility and strength of the thumb, make possible two different hand grips that characterize our species: the precision grip, in which objects are held between the tips of the fingers and the tip of the thumb, and the power grip, in which the fingers and thumb are wrapped fully around the object (Napier, 1960; Napier, 1962; Napier, 1965; Marzke, 1983; Marzke, 1997; Susman, 1979; Susman, 1998). These grips are generally thought to be crucial to the great manipulative skills of humans and are usually associated with tool manufacture and use (Napier, 1965; Marzke, 1997; Susman, 1998; Young, 2003). Manual manipulation is central to human behavior and has clearly played a crucial role in the evolution of the human hand. In contrast, the long hands of the other apes are thought to be an adaptation for arboreal climbing and foraging on large-diameter branches (Susman, 1979; Inouye, 1992).

Recently, many of the derived proportions of the human hand have also been suggested to be a pleiotropic result of selection on the foot for terrestrial locomotion (Alba et al., 2003; Rolian et al., 2010). Hands and feet are serially homologous structures that share similar developmental pathways. This raises the possibility that the proportions of human hands and feet coevolved. The selection for economical walking and running that led to the evolution of a long robust big toe and short lateral toes may have resulted in similar

changes in the proportions of the hand that coincidentally facilitated improved manual dexterity.

A third possibility is that the proportions of the human hand are the result of sexual selection for improved striking performance during hand-to-hand combat by males. The bones of the human hand are proportioned in a way that may provide supportive buttressing that protects the hand from injury when striking with a fist (Fig. 2). We define buttresses as contacts between the digits or between the digits and palm that stiffen the fist and/or transmit force from the digits to the palm, wrist and forearm. Two buttresses are formed when full flexion of digits 2–5 at the metacarpophalangeal (MCP), proximal interphalangeal and distal interphalangeal joints brings the primary phalangeal pads into contact with the central palm and the palmar pads of the proximal phalanges (the phalangeal–palmar buttresses) (Fig. 2). The third and fourth buttresses are formed by flexion, adduction and opposition of the thumb, which rotates the thenar eminence towards the palm to abut the dorsal (i.e. nail) surface of the distal phalanges of the flexed digits 2 and 3, and the thumb itself wraps around the middle phalanges of digits 2 and 3. It is through a precise integration of the derived proportions of the human hand that these four buttresses occur simultaneously. In what we call the protective buttressing hypothesis, the proportions of the human fist function to strengthen and stabilize the hand during striking such that: (1) the hand is held in a stiffer posture that can be used to deliver a strike with more force and/or energy; (2) potentially damaging hyperflexion of the MCP joints does not occur; (3) metacarpals 2–5 are loaded primarily in long-axis compression rather than bending; and (4) peak loads on metacarpals 2–5 are

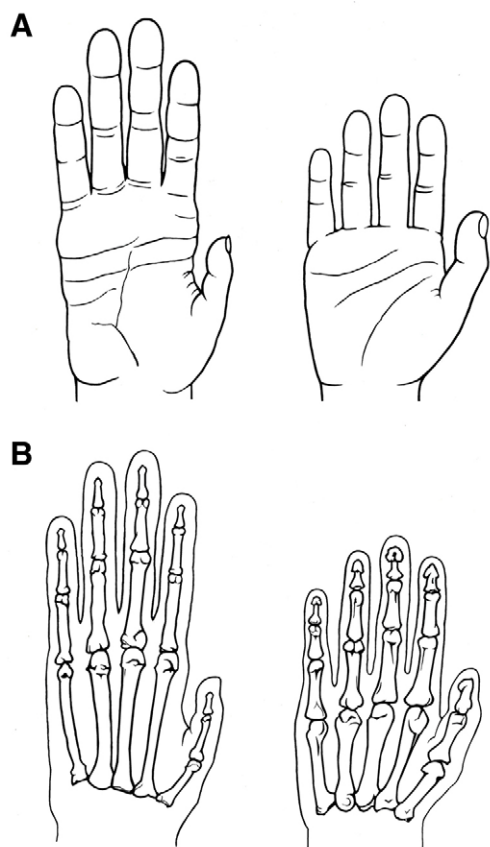


Fig. 1. Comparison of the external (A) and skeletal (B) proportions of the hands of chimpanzees (left) and humans (right). Redrawn from Young (Young, 2003).

reduced as a result of energy transfer from the distal phalanges of digits 2 and 3, through the first metacarpal to the wrist and to the flexor and adductor muscles of the thenar eminence and thumb (Fig. 3). Thus, the proportions of the human hand may have evolved in response to selection to make the hand a more effective weapon, allowing competing males to strike with greater force and power while greatly reducing the risk of injury to the hand.

The protective buttressing hypothesis is entirely compatible with the hypotheses that the derived proportions of human hands evolved: (1) in response to selection for increased precision and strength of grasping associated with manual manipulation (Napier, 1965; Marzke, 1983; Marzke, 1997; Susman, 1979; Susman, 1998) and (2) in response to selection on the foot for terrestrial locomotion, which resulted in coevolution of the hand (Alba et al., 2003; Rolian et al., 2010). It seems reasonable that selection for improved terrestrial locomotion, manual dexterity and fighting performance may all have played a role in the evolution of the proportions of the hands of hominins.

To clarify how energy may be transferred from the distal phalanges of digits 2 and 3 through the thumb, consider that during the impact of a punching strike, flexion of digits 2 and 3 at the MCP joints applies force on the thenar eminence that acts to abduct and reposition the first metacarpal (Fig. 3). This is likely to: (1) transfer force through the first metacarpal to the wrist, partially unloading the second and third metacarpals; and (2) dissipate energy of the strike through stretching of the adductor and flexor muscles and tendons of the thenar eminence and thumb, specifically the opponens

pollicis, adductor pollicis, flexor pollicis brevis and flexor pollicis longus muscles. Thus, in addition to protectively stiffening the joints of the hand during a strike, the buttressing of the human fist may provide a mechanism of shock absorption through energy dissipation in the adductor and flexor muscles of the thumb.

The skeletal proportions of the hand of other great apes are poorly suited for buttressing of digits 2 and 3 by the thenar eminence and thumb. In chimpanzees, for example, the greater length of the hand, compared with humans, is largely the result of the length of the metacarpals and the proximal phalanges of digits 2–5 (Fig. 1). In contrast, the middle and distal phalanges are of similar absolute length in chimpanzees and humans. However, it is the middle and distal phalanges that bridge the distance between the distal end of the proximal phalanges and the thenar eminence in the human fist. Thus, the proportions of the skeletal elements of digital rays 2 and 3 of chimpanzees are poorly suited to human-like buttressing by the thenar eminence and thumb. Additionally, both the thenar eminence and thumb are relatively small in chimpanzees, further limiting the capacity of the first digit to provide buttressing of the fist. An additional factor that would limit the effectiveness of buttressing in the hands of other great apes is the relatively limited strength of the muscles responsible for adduction and flexion of the thumb. The intrinsic muscles of the thumb have greater physiological cross-sectional areas (PCSAs) and larger muscle moment arms in humans than in chimpanzees, such that the total potential torque these muscles can apply to the thumb is estimated to be 2.2-fold greater in humans (Marzke, 1997; Marzke et al., 1999; Ogiwara et al., 2005). Furthermore, the flexor pollicis longus muscle, which is ~22% of the total thumb muscle PCSA in humans (Marzke, 1997; Marzke et al., 1999), is absent or poorly developed in other great apes (Susman, 1998; Straus, 1942).

The importance of a clenched fist to human aggression is reflected in the role that it plays in threat displays. Threat displays provide important clues to the weapons used in fighting. Game theory modeling of aggressive encounters suggests that threat displays usually provide an honest indication of one's fighting ability (Maynard Smith and Price, 1973; Parker, 1974; Enquist, 1985; Szamado, 2008; Szalai and Szamado, 2009). Importantly, it is usually the first step in a species' fighting technique that is used to threaten (Szamado, 2008; Walther, 1984). Although descriptions of how humans fight with their arms are rare in the literature, striking with fists appears to be universal among Europeans (Darwin, 1899), it is commonly employed in the Asian fighting styles of Karate and Kung Fu (e.g. the Chinese martial art Xingyiquan, which means 'form and intent fist'), it is used in fighting competitions by at least one group of Native Americans, the Yanomamo (Chagnon, 1968), and it is the dominant striking mode used in modern mixed martial arts competitions. Granted, it is difficult to assert that the fist is our instinctually preferred weapon, but it has been noted that infants often use a 'closed hand' to express anxiety and distress (Legerstee et al., 1990). Thus, the formation of a fist in response to stressful or anxiety inducing stimuli likely reflects a willingness to use physical force to resolve disputes (Darwin, 1899; Schubert and Koole, 2009; Morris, 1977; Crouner et al., 2005) and suggests that fists are one of the primary weapons of humans.

Central to the possibility that the derived proportions of the human hand have been influenced by selection for fighting performance is the ubiquity and importance of intense male–male physical competition among all species of extant great apes (Wrangham and Peterson, 1996; Carrier, 2007; Puts, 2010). Coalitional killings have been reported from eight out of 10 chimpanzee study populations (Wrangham, 1999; Boesch et al., 2008), and the deaths can represent

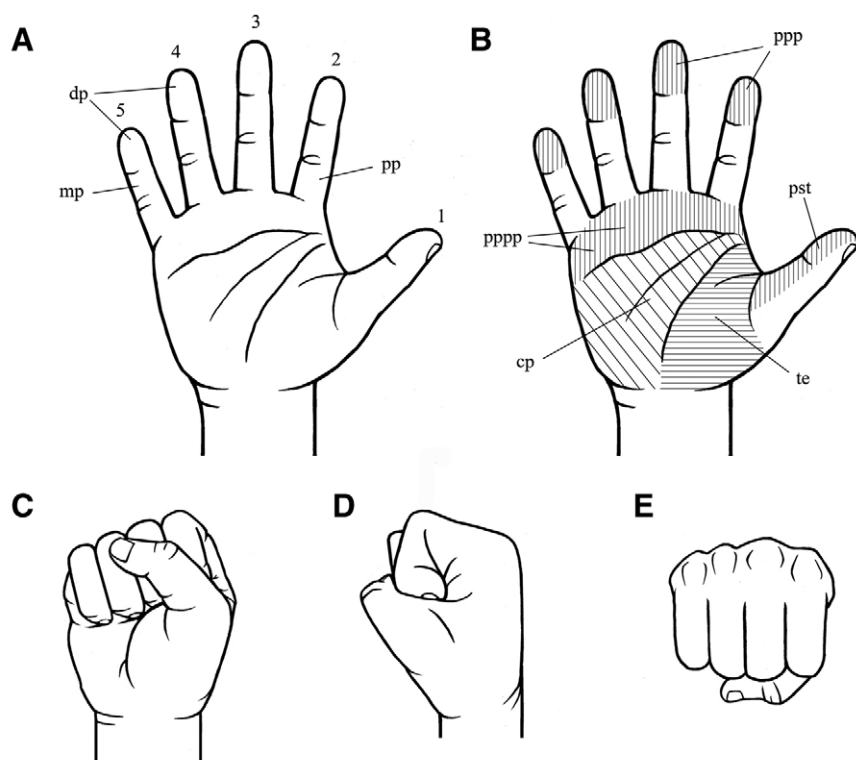


Fig. 2. Illustrations of the human hand showing the anatomical basis of supportive buttressing of the fist. (A) Palmar surface of the hand. Digits are indicated by numbers 1–5. Labeling identifies the distal phalanges (dp), middle phalanges (mp) and proximal phalanges (pp). (B) Digital and palmar surfaces that function in buttressing of the fist, following the nomenclature of Biegert (Biegert, 1959): ppp, primary phalangeal pads; pppp, palmar pads of the proximal phalanges; cp, central palm; te, thenar eminence; and pst, palmar surface of the thumb. (C) Palmar view of the fist showing the buttressing of the distal tips of the phalanges against the central palm and buttressing of the thenar eminence and thumb against the dorsal surfaces of digits 2 and 3. (D) Radial (i.e. lateral) view of the fist showing buttressing of the tip of digit 2 against the central palm and the palmar pad of its proximal phalanx and buttressing of the thumb against the dorsal surface of digit 2. (E) View of the striking surface of the fist.

a significant proportion of the population (Wrangham, 1999; Watts et al., 2006). Male–male aggression among bonobos appears similar in many ways to that of chimpanzees, but of a lower intensity and without coalitional killing (Kano, 1992; Furuichi, 1997; Hohmann and Fruth, 2003). Mature male orangutans are reported to be totally intolerant of each other (Galdikas, 1985); for example, of two observed encounters between adult males in the presence of adult females, both ‘entailed considerable physical violence’ (Galdikas, 1985). In gorillas, male–male aggression during intergroup encounters is common. Harcourt (Harcourt, 1978) reported that violent displays occur during 80% of these encounters and fights between males occur during 50% of the encounters. Gorillas also display twice the prevalence of cranial trauma (11%) as chimpanzees, and this trauma is thought to be primarily associated with male–male aggression (Jurmain, 1997). Thus, because the mating systems of great apes, including humans, are characterized by male–male competition (Wrangham and Peterson, 1996; Plavcan, 2000), which can subject males to intense sexual selection on fighting performance (Puts, 2010), it is appropriate to question the role that this selection may have had on the evolution of the human hand.

The goal of this study was to test the hypothesis that the proportions of the human hand make it an effective weapon. To test the hypothesis that striking with a fist provides a performance advantage, we measured the peak forces, force impulses and rate of change of acceleration (jerk) of maximum effort strikes of subjects striking with a fist and an open hand in forward, side and overhead strikes. To test the hypothesis that a fist provides protective buttressing of the hand during striking, we measured (1) the static stiffness of the second MCP joint and (2) static force transfer from digits 2 and 3 to digit 1 in fully buttressed and unbuttressed fist postures (Fig. 4). The protective buttressing hypothesis predicts that the resistance to forces that tend to flex the digits at the MCP joints will be greater, that is the joints will be stiffer, when the fist is buttressed than when it is unbuttressed. The hypotheses of energy

transfer from the phalanges of digits 2 and 3, through the thenar eminence to the wrist and flexor and adductor muscles of the thumb predicts that a larger force can be supported by the phalanges of digits 2–5 when the fist is fully buttressed than when it is unbuttressed.

## MATERIALS AND METHODS

### Subjects and protocol

To test the hypothesis that striking with a fist provides a performance advantage, we measured the peak forces, force impulses and peak rate of change of acceleration (jerk) of maximum effort strikes of subjects striking with a fist and an open hand in forward, side and overhead strikes. To test the hypothesis that a fist provides protective buttressing of the hand during striking, we measured the static stiffness of the digits and static force transfer from digits 2 and 3 to the wrist in buttressed and unbuttressed postures. All subjects were healthy males who had received training in boxing or martial arts prior to the study. A total of 12 subjects participated in the study, but not all individuals were subjects in each of the three experiments. Each of the experiments had a sample size of 10 subjects. Subjects gave informed consent, and all procedures were approved by the University of Utah Internal Review Board.

### Striking performance with a closed fist versus an open palm

To measure the forces and resulting acceleration of maximum effort strikes when striking with a fist and an open hand, subjects struck an instrumented mass (i.e. punching bag) close to its center of mass. The punching bag had a mass of 45.45 kg and was suspended from the ceiling of the laboratory with chains 2.0 m long. We measured acceleration of the bag with an Endevco model 7290A-10 Microtron accelerometer (San Juan Capistrano, CA, USA) attached to the outside of the bag lateral to its center of mass. The accelerometer had a working range of –18 to +19 g. Digital data were collected on a computer with a sampling rate of 4000 Hz. Compliance of the target was necessary to avoid injury of the subjects’ hands and arms.



Fig. 3. Illustration of the change in shape of the fist that occurs on impact during a strike. The gray lines illustrate the posture of the digits before impact and the black lines the posture immediately after impact. During impact, the force (gray arrows) applied to the proximal phalanges of digits 2 and 3 produces flexion at the metacarpo-phalangeal joints. Flexion of these digits transfers force to the thenar eminence, abducting the first metacarpal. Through this linkage, we hypothesize that force (black arrow) is transferred through the first metacarpal to the wrist and energy is dissipated as a result of stretching of the adductor and flexor muscles of the thenar eminence and thumb.

In this regard, a punching bag worked well as a target mass. To reduce the energy lost in deformation of the bag, a stiff, semi-circular support that ran the length of the bag was firmly attached to the back of the bag with duct tape. Nevertheless, because some energy was absorbed by compliance of the bag, and was not converted to acceleration, the results of this analysis represent an underestimate of the actual forces applied by the subjects. Ten subjects (body mass  $84.0 \pm 11.9$  kg; age  $36.3 \pm 9.7$  years) participated in this experiment.

Subjects warmed up and became familiar with the punching transducer by striking with sub-maximal effort. Once warmed up and familiar with the task, subjects were asked to strike the transducer as hard as possible three times with a closed fist and three times with an open palm, for each of three different strikes: overhead, side and forward. Thus, each subject struck the bag a total of 18 times. To avoid muscular fatigue, subjects rested ~60 s between strikes and the sequence of strikes was alternated randomly

among the subjects, with each subject performing one fist and one palm strike in a given striking mode (e.g. overhead) and then switching to the next striking mode. For the open hand strikes, subjects were instructed to strike the bag with the full hand, including both the palm and fingers. The extent to which this occurred was not documented. However, because the bag was deformable, pressure was applied to the bag through the whole ventral surface of the hand.

The overhead strikes consisted of the 'hammer fist', in which subjects hit the transducer with the medial (i.e. digit 5) side of the fist, and the 'overhead slap', in which the subjects struck the transducer with the palm of their hand. For the side strikes, subjects were instructed to 'side punch' the transducer with the lateral (i.e. digit 1) side of their fist and 'side slap' the transducer with the palm of their hand. The forward strikes consisted of a typical boxing 'forward punch', in which the subjects struck the transducer with the proximal phalanges of their fist (digits 2–5), and the 'palm shove', in which the subjects struck the transducer in a forward strike with the palm of their open hand. We did not instruct the subjects as to specific arm or body motions during striking. We simply asked them to hit the target as hard as possible.

We measured the acceleration of the bag and then multiplied the instantaneous acceleration of the bag by the bag's mass to obtain the instantaneous force and determined the peak force (N) and force impulse (Ns) of each strike. We also determined the peak jerk [rate of change of acceleration ( $\text{ms}^{-3}$ )] experienced by the bag during the period of increasing acceleration. Tests of difference were performed with paired Student's *t*-test and a simple Bonferroni correction given the three striking modes: overhead, side and forward. Thus, we assumed the results were significantly different when the *P*-value was less than 0.017. We used a one-sided test for significance given the hypothesis that striking with a fist would be more effective than striking with an open palm.

#### Effect of buttressing on flexural stiffness of the MCP joint of digit 2

We measured the submaximal stiffness of the second MCP joint during static loading in three hand postures: formed fist (i.e. fully buttressed), phalangeal-palmar buttress with no buttressing from the thenar eminence and thumb, and unbuttressed (Fig. 4). With the hand in one of these three postures, subjects pushed on a force transducer (Interface SML-200, Scottsdale, AZ, USA) with the dorsal surface of the distal end of the first phalanx of digit 2 (Fig. 5A) and we recorded the applied force and the displacement of the second metacarpal parallel to the applied force vector that occurred as a result of flexion of the second MCP joint. Displacement of the second metacarpal was measured with a linear variable differential transformer (model 7306-W2-A0, Pickering and Co., Plainview, NY, USA). Each subject applied force, in each of the three hand postures, three times. Subjects were asked to push hard on the

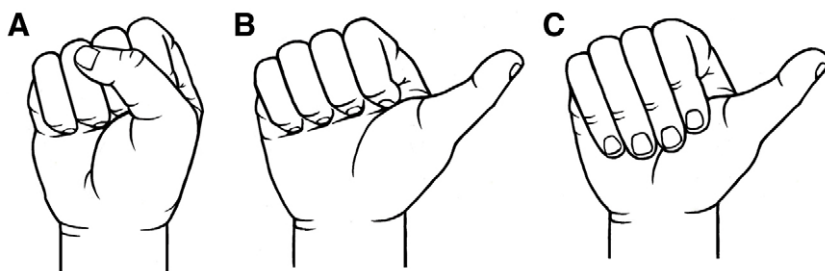


Fig. 4. Illustrations of the hand postures used in this investigation. (A) Normal fully buttressed fist in which tips of the fingers abut the central palm and the palmar pads of the proximal phalanges, the thenar eminence supports the distal phalanges of digits 2 and 3, and the thumb supports the middle phalanges of digits 2 and 3. (B) The buttressing from the thenar eminence and thumb is removed but the phalangeal-palmar buttress remains. (C) The unbuttressed posture, in which the thenar eminence and thumb are abducted and distal phalangeal pads loosely contact the proximal palm.



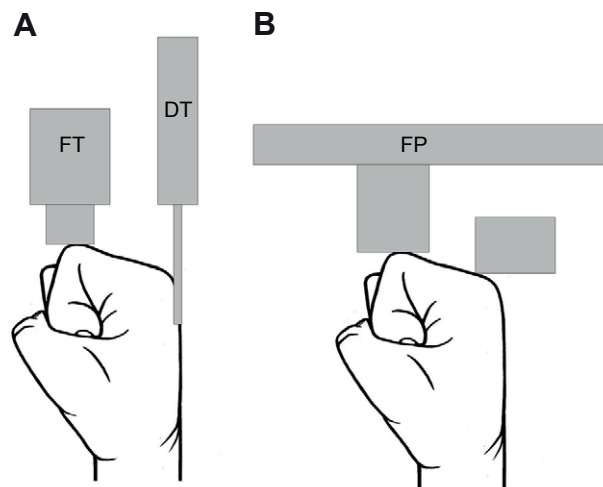


Fig. 5. Illustration of the methods used to measure the effect of buttressing on (A) the stiffness of the second metacarpo-phalangeal (MCP) joint and (B) the force transfer to the wrist from digits 2 and 3 via the thenar eminence. To measure the stiffness of the second MCP joint, subjects pushed on a force transducer (FT) with the distal end of their second proximal phalanx (A). A displacement transducer (DT), attached to the dorsal of the second knuckle, measured the displacement of the hand and therefore the change in angle of the second MCP joint. To measure force transfer from the digits to the wrist, subjects applied force to two blocks (B). The block under the distal end of the proximal phalanges rested on a force plate (FP), whereas the block under the knuckles was supported by a beam resting on the floor.

transducer, but not maximally. Ten subjects (body mass  $83.3\pm10.3$  kg; age  $38.6\pm12.4$  years) participated in this experiment. We calculated the stiffness of the joint ( $\text{Nm rad}^{-1}$ ) by determining the slope of the initial linear portion of the loading–displacement curve using least-squared regression. Average stiffness of the three trials from each subject was used in the analysis. Tests of difference were performed with paired Student’s *t*-test and a simple Bonferroni correction for the two comparisons of phalangeal–palmar buttressed versus unbuttressed and fully buttressed versus phalangeal–palmar buttressed. Thus, we assumed the results were significantly different when the *P*-value was less than 0.025. We used a one-sided test for significance given the hypothesis that increased buttressing would increase the stiffness of the joint.

**Effect of buttressing on force transfer to wrist from digits 2 and 3 via digit 1**

To estimate the extent to which the force applied to the fist in a strike can be transferred from digits 2 and 3, via thenar eminence, to the wrist, we measured the percentage of upper body weight that subjects could support with their proximal phalanges under three conditions: buttressed fist (Fig. 2A), unbuttressed (Fig. 2C) with the wrist stabilized such that the palm was held parallel and in line with the radius and ulna, and unbuttressed with the wrist unstabilized. In the unstabilized wrist posture, the subjects allowed their wrist to extend into a collapsed position such that the passive stiffness of the MCP joints applied force through the proximal phalanges to the force plate. Subjects adopted a one-arm push-up posture, supporting their upper body weight with the fist of their right hand (Fig. 5B) resting on a set of two wooden blocks. The block supporting the knuckles (i.e. MCP joints of digits 2–5) applied force to the floor, whereas the block supporting the distal ends of the proximal phalanges applied force to a force plate (Kistler, 9281B SN; Novi, MI, USA). In this way we were able to distinguish

the force applied by the proximal phalanges *versus* the force applied by the knuckles of the metacarpals. To determine the percentage of body weight supported by the arm of each subject in the one-armed push-up posture, subjects placed their fist directly on the force plate and adopted the one-armed push-up posture five times. The average force from these five trials was assumed to be the weight supported by the arm in the experimental trials. Subjects then adopted the one-arm push-up posture on the two blocks to apply force to the force plate through their proximal phalanges of digits 2–5. Each subject applied force, in each of the three hand postures, three times. The hypothesis of energy transfer from phalanges 2 and 3, through the thenar eminence, to the wrist and flexor and adductor muscles of the thumb predicts that a larger force can be supported by the phalanges of digits 2–5 when the fist is held in a fully buttressed posture than when it is held in an unbuttressed posture. The average of the three trials for each subject was used in the analysis. Ten subjects (body mass  $75.5\pm20.8$  kg; age  $33.4\pm13.9$  years) participated in this experiment.

Tests of difference were performed with paired Student’s *t*-tests and a simple Bonferroni correction for the two comparisons of buttressed fist *versus* unbuttressed with the wrist stabilized, and buttressed fist *versus* unbuttressed with the wrist unstabilized. Thus, we assumed the results were significantly different when the *P*-value was less than 0.025. We used a one-sided test for significance given the hypothesis that buttressing would increase the force that can be supported by digits 2–5.

**RESULTS**

**Striking performance with a closed fist versus an open palm**

Peak forces did not differ between the closed fist and open palm trials for the overhead, side or forward strikes (Table 1). Similarly, no difference was observed in force impulse between the closed fist and open palm trials for the overhead and forward strikes. However, the force impulse of the closed fist side punches was 15.0% greater than that of the side slaps. Additionally, maximum jerk did not differ between the closed fist and open palm trials (Table 1).

**Effect of buttressing on flexural stiffness of the MCP joint of digit 2**

No differences among the three fist postures were observed in the amplitude of force applied by the subjects in the MCP joint stiffness test (Table 2). However, the degree to which the MCP joint of the

Table 1. Mean and standard deviations of peak force, force impulse and jerk of maximum effort strikes made with an open palm and with a fist

	Open palm	Fist	<i>P</i>
Peak force (N)			
Overhead	4591.7±1867.2	4365.4±1044.9	0.335
Side	4582.3±1418.5	5351.4±1473.5	0.131
Forward	5768.2±1285.2	5811.6±1706.6	0.453
Force impulse (Ns)			
Overhead	26.1±4.7	26.9±3.5	0.223
Side	32.6±9.6	37.5±6.6	<b>0.016</b>
Forward	44.3±8.8	42.7±2	0.296
Jerk ( $\text{m s}^{-3}$ )			
Overhead	87,230±70,711	66,734±24,233	0.172
Side	58,749±34,327	67,924±57,390	0.379
Forward	57,140±35,657	63,059±49,224	0.309

*P*-values indicate differences between open palm and fish strikes. Significant *P*-values (<0.017) are in bold.

Table 2. Mean and standard deviations of applied force, displacement and stiffness of the second metacarpo-phalangeal joint during static loading of the proximal phalanx of digit 2 in three hand postures

	Unbuttressed	No thenar eminence	Buttressed	<i>P</i>	
				Unbuttressed vs. no thenar eminence	No thenar eminence vs. buttressed
Force (Nm)	4.54±2.04	5.27±2.04	4.96±2.28	0.080	0.043
Displacement (rad)	0.282±0.104	0.178±0.075	0.112±0.054	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Stiffness (Nm rad <sup>-1</sup> )	14.0±6.3	27.4±13.9	49.5±31.1	<b>0.001</b>	<b>0.002</b>

The hand postures used in this test are illustrated in Fig. 2.

Significant *P*-values (<0.025) are in bold.

second digit flexed did vary between the buttressed and unbuttressed fist postures. The proximal phalanx of the second digit underwent 58% more displacement in the unbuttressed posture than in the phalangeal-palmar buttressed posture and 58% more displacement in the phalangeal-palmar buttressed posture than in the fully buttressed posture. The second MCP joint exhibited an average 96% greater stiffness in the phalangeal-palmar buttressed posture than in the unbuttressed posture and was 94% stiffer in the buttressed than in the phalangeal-palmar buttressed posture. Thus the MCP joint of digit 2 is approximately fourfold stiffer in the fully buttressed than in the unbuttressed posture.

#### Effect of buttressing on the ability of the proximal phalanges to transmit 'punching' force

With a fully buttressed fist, subjects were able to support 79.4±9.2% (mean ± s.d.) of their upper body weight on their proximal phalanges. When the fist was unbuttressed and the wrist was stabilized, such that the palm of the hand was held in line with the long-axis of the forearm, the subjects were able to support only 32.7±12.3% of upper body weight on the proximal phalanges. When the fist was unbuttressed and the wrist was allowed to collapse in extension, the subjects were able to support 58.6±20.6% of upper body weight on their proximal phalanges. The percentage of upper body weight supported by the proximal phalanges was significantly greater in the buttressed fist than in the unbuttressed stabilized fist ( $P<0.0001$ ) and in the unbuttressed collapsed fist ( $P=0.0087$ ).

#### DISCUSSION

Contrary to our expectations, striking with a clenched fist appears to provide little or no performance advantage in terms of the force applied to the target. The force and force impulse of both forward and overhead strikes were not different when the subjects struck with a fist or an open palm. Our subjects did demonstrate a 15% increase in force impulse in side strikes with a fist, but the peak force of side strikes with a fist were not significantly greater than side slaps. Additionally, the maximum rate of change acceleration (i.e. jerk), which has been implicated in both traumatic brain and musculoskeletal injury (Ivancevic, 2009a; Ivancevic, 2009b), was not different when the subjects struck with a fist or an open palm.

Although the forcefulness of a strike can be important to the outcome of a fight (e.g. accelerating the body, knocking an opponent off their feet; or accelerating the head, causing unconsciousness or a concussion), local tissue damage, such as bone fracture and contusion, is produced not by force but by stress (force per area) (Farlow et al., 2000). Given that our subjects produced similar peak forces and force impulses when striking with fists and palms, striking with a fist increases the peak stress imposed on the target. We do not know the degree to which the applied pressure was uniform under the hand; however, because the bag was deformable we can

be confident that pressure was applied by the whole ventral surface of the hand, including both the palm and the fingers. The striking surface area of a fist is less than one-third the area of the whole hand and ~60% of the area of the palm. This means that if the total force applied in a strike is the same, then the stress in the targeted tissue will be 1.7 to 3.0 times greater in a fist strike than in a palm strike. Thus, although striking with a fist appears not to result in more forceful strikes, fists increase the peak stresses that are imposed on the target and, therefore, the potential for injury.

Possibly the most significant result of this study is the finding that the structure of the human fist provides protective buttressing of the metacarpals, MCP joints and phalanges. Compared with the unbuttressed fist posture, stiffness of the second MCP joint doubled when the distal phalangeal pads were buttressed against the central palm and the palmar pads of the proximal phalanges. Stiffness of this joint doubled again when the thumb and the thenar eminence were rotated to firmly grip the dorsal surface of the distal phalanges of digits 2 and 3. Presumably, this fourfold increase in stiffness of the second MCP joint reflects significant increases in the stiffness of the MCP joints of digits 3–5. Increased MCP joint stiffness protects the MCP joints from extreme hyperflexion and likely reduces resulting bending moments on the metacarpals when the fist strikes a target. The subjects were able to support 79% of their upper body weight on their proximal phalanges, rather than their metacarpals, when the fist was fully buttressed. In contrast, when the fist was unbuttressed and the wrist was stabilized, the subjects were able to support only 32% of upper body weight on the proximal phalanges. This illustrates the extent to which force from digits 2 and 3 can be transferred through the thumb and thenar eminence to the wrist. Thus, the buttressing of the hand that is intrinsic to a formed fist: (1) protects the MCP joints from hyperflexion; (2) secures the individual digits in a tight configuration that prevents potentially harmful strain at the interphalangeal joints; (3) presumably helps to keep the metacarpals loaded in long-axis compression rather than bending; and (4) makes possible a transfer of energy from digits 2 and 3, through the thenar eminence, to the wrist, unloading the metacarpals. This protective buttressing requires an integration of the proportions of the skeletal elements of the hand and may represent the primary advantage in striking with a fist.

Precision pad-to-pad grip could have evolved for manual manipulation in ways that are not compatible with a buttressed fist. A precision grip could have evolved through: (1) a shortening of the metacarpals and fingers and a lengthening of the thumb, as occurred in the hominin lineage; (2) a substantial lengthening of the thumb ray only; or (3) a predominant shortening of either the finger rays only or metacarpals 2–5 only. Importantly, these alternatives do not require strict coordination of the relative lengths of the phalanges or coordination of the length of the metacarpals (2–5) with the length of the first metacarpal.

In contrast to the geometry necessary for precision grip, a buttressed fist requires specific proportions among the skeletal elements of the hand. The fist of humans is characterized by buttressing of the tips of the distal phalanges against the palm and the pads of the distal phalanges against the palmar skin over the proximal phalanges. This dual contact requires integration of the relative lengths of the three phalanges and an integration of the lengths of the fingers with their diameter. If the phalanges of digits 2–5 were longer, as in members of the genus *Pan*, the tips of the distal phalanges could abut the palm, but the primary phalangeal pads would not abut the palmar pads of proximal phalanges, leaving a destabilizing space between the proximal and distal phalanges. If the proximal phalanges were too long relative to the distal phalanges, the tips of the fingers would not reach the palm. If the middle phalanges were too long, the primary phalangeal pads would also not abut the palmar pads of the proximal phalanges. Additionally, significant increases or decreases in the length of the distal phalanges would compromise the 90 deg angle between the metacarpals and proximal phalanges that forms the striking surface of the fist. As stated before, the length of the first metacarpal in relation to the lengths of metacarpals 2 and 3 is necessary for the precise integration that allows buttressing with the thenar eminence. Thus, the geometry of a fully buttressed fist provides a clear explanation for the specific skeletal proportions of the human hand.

Specialization of the hand for punching during the evolution of early hominins is consistent with proposed anatomical specialization for physical aggression (Carrier, 2004; Carrier, 2007; Carrier, 2011) and the apparent patterns of sexual dimorphism in these fossil species. Most species of early hominins (*Australopithecus* and *Paranthropus*) appear to have had pronounced sexual dimorphism in body size, with males being bigger than females (McHenry, 1996; Gordon et al., 2008; but for an alternative view see Reno et al., 2010). Among mammals, species in which males are larger than females tend to have polygynous mating systems and males compete physically for reproductive access to females (Clutton-Brock et al., 1982; Jarman, 1983; Parker, 1983; Alexander et al., 1979; Andersson, 1994). Specifically among primates, there is a positive correlation between size sexual dimorphism and the number of adult females per adult male in breeding groups (Clutton-Brock et al., 1977). Analyses of anthropoid primates show that size sexual dimorphism is strongly associated with both male–male competition levels and the ratio of mature males to females that are ready to mate (Plavcan and van Schaik, 1997a; Plavcan and van Schaik, 1997b; Plavcan, 1999; Plavcan, 2004). Thus, the evidence for size sexual dimorphism in early hominins suggests the presence of polygynous mating systems with high levels of male–male competition.

The forelimbs of great apes exhibit relatively high levels of sexual dimorphism. In *Australopithecus afarensis*, for example, the difference between large and small ulnae, radii and capitates is as great or greater than that between male and female means of the most dimorphic extant apes (McHenry, 1986; McHenry, 1991; McHenry, 1996). Forelimbs also appear to have been relatively dimorphic in both *A. africanus* and *Paranthropus boisei* (McHenry, 1996). In lowland gorillas, the greatest sexual dimorphism is in the weight of the forelimbs, the forelimb trunk binding muscles and the epaxial muscles (Zihlman and McFarland, 2000). In addition, in humans, the arms and upper body are more sexually dimorphic than the legs (Price et al., 2011) and the greatest dimorphism in size appears to be in the forearm and hand (Lindgard, 1953). Additionally, as would be expected if human hand proportions evolved as a result of sexual selection, there is also dimorphism in

the shape of the hand. The ratio between the lengths of the second and fourth digits is lower in males than in females (Manning et al., 1998). This ratio is negatively correlated with levels of prenatal and adult testosterone (Manning et al., 1998), performance and success in football (soccer) (Manning and Taylor, 2001), and perceived male dominance (Neave et al., 2003). Importantly, among mammals, sexual dimorphism is often greatest in those characters that enhance a male's capacity to dominate other males (Parker, 1983; Andersson, 1994; Clutton-Brock and Harvey, 1977). Thus, the relatively high levels of sexual dimorphism in the arm and hand are consistent with the hypothesis that the proportions of the human hand have been influenced by sexual selection.

The skeletal proportions that make the buttressed fist of modern humans possible appear to have evolved at approximately the same time as habitual bipedalism. The earliest habitual biped *Orrorin tugenensis*, dating from 6 million years ago (Pickford et al., 2002; Richmond and Jungers, 2008), had a thumb anatomy that is more human-like than that of australopiths and displayed typical human-like features related to precision grasping (Almécija et al., 2010). In contrast, the hands of the 4.4-million-year-old hominin, *Ardipithecus ramidus*, are suggested to have been adapted for climbing and possibly foraging in distal branches, and are more similar in proportion to those of monkeys than to those of modern great apes and humans (Lovejoy et al., 2009; Crompton et al., 2010). Nevertheless, the earliest undisputed hominins, the australopiths, had manual proportions very similar to those of modern humans. Recent analysis of *A. afarensis* from locality AL 333/333w (Hadar, Ethiopia) indicates that this species possessed overall manual proportions, including an increased thumb/hand relationship, that '... is fully human and would have permitted pad-to-pad human-like precision grip capability' (Alba et al., 2003). Based on the relative proportions of metacarpals 1–4, *Australopithecus africanus* also appears to have had human-like hand proportions (Green and Gordon, 2008). Well-preserved pollical metacarpal and distal phalangeal bones from the australopith *Paranthropus robustus* indicate that this 1.8-million-year-old contemporary of *Homo* also had hands that were adapted for precision grasping (Susman, 1994; Susman, 1988). A nearly complete hand of *Australopithecus sediba* (1.98 million years ago) demonstrates that this species had short fingers, a long thumb with a human-like palmar pad and a mobile proximal pulp, and a strong flexor pollicis longus muscle, all features that have been associated with a powerful, precision grip (Kivell et al., 2011). Thus, the evolution of human-like manual proportions were largely coincident with the evolution of habitual bipedalism. This is likely the result of selection for increased manual dexterity being released from the constraining influence of selection for performance in an arboreal environment (Alba et al., 2003). Alternatively, it has been suggested that the hand proportions of hominins may partially, or largely, be a pleiotrophic result of selection on the foot for terrestrial locomotion (Alba et al., 2003; Rolian et al., 2010). A third reason that human-like manual proportions appear in the fossil record coincident with evidence of habitual bipedalism is that sexual selection for improved fighting performance may have contributed to the evolution of both (Carrier, 2011; present study).

There appears to be a paradox in the evolution of the human hand. It is arguably our most important anatomical weapon, used to threaten, beat and sometimes kill to resolve conflict. Yet it is also the part of our musculoskeletal system that crafts and uses delicate tools, plays musical instruments, produces art, conveys complex intentions and emotions, and nurtures. Starting with the hand of an arboreal great ape ancestor, it is possible to imagine a number of



evolutionary transformations that would have resulted in a club-like structure adapted for fighting. Similarly, as suggested above, there are a number of alternative hand proportions that are compatible with enhanced manual dexterity. There may, however, be only one set of skeletal proportions that allows the hand to function both as a mechanism for precise manipulation and as a club for striking. More than any other part of our anatomy, the hand represents the identity of *Homo sapiens*. Ultimately, the evolutionary significance of the human hand may lie in its remarkable ability to serve two seemingly incompatible, but intrinsically human, functions.

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## REFERENCES

- Alba, D. M., Moyà-Solà, S. and Köhler, M. (2003). Morphological affinities of the *Australopithecus afarensis* hand on the basis of manual proportions and relative thumb length. *J. Hum. Evol.* **44**, 225-254.
- Alexander, R. D., Hoogland, J. L., Howard, R. D., Noonan, K. M. and Sherman, P. W. (1979). Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates and humans. In *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective* (ed. N. A. Chagnon and W. Irons), pp. 402-435. New Scituate, MA: Duxbury Press.
- Almécija, S., Moyà-Solà, S. and Alba, D. M. (2010). Early origin for human-like precision grasping: a comparative study of pollical distal phalanges in fossil hominins. *PLoS ONE* **5**, e11727.
- Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Ashley-Montagu, F. M. (1931). On the primate thumb. *Am. J. Phys. Anthropol.* **15**, 291-314.
- Biegert, J. (1959). Die Ballen, Leisten, Furchen und Nägel von Hand und Fuß der Halbaffen. *Z. Morphol. Anthropol.* **49**, 316-409.
- Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y. and Normand, E. (2008). Intergroup conflicts among chimpanzees in Taï National Park: lethal violence and the female perspective. *Am. J. Primatol.* **70**, 519-532.
- Carrier, D. R. (2004). The running-fighting dichotomy and the evolution of aggression in hominids. In *From Biped to Strider: The Emergence of Modern Human Walking, Running, and Resource Transport* (ed. J. Meldrum and C. Hilton), pp. 135-162. New York, NY: Kluwer/Plenum Press.
- Carrier, D. R. (2007). The short legs of great apes: evidence for aggressive behavior in australopithecids. *Evolution* **61**, 596-605.
- Carrier, D. R. (2011). The advantage of standing up to fight and the evolution of habitual bipedalism in hominins. *PLoS ONE* **6**, e19630.
- Chagnon, N. A. (1968). *Yanomamo: The Fierce People*. New York, NY: Holt, Rinehart and Winston.
- Christel, M. (1993). Grasping techniques and hand preferences in Hominoidea. In *Hands of Primates* (ed. H. Preuschoft and D. Chivers), pp. 91-108. New York, NY: Springer-Verlag/Weins.
- Clutton-Brock, T. H. and Harvey, P. H. (1977). Primate ecology and social organization. *J. Zool.* **183**, 1-39.
- Clutton-Brock, T. H., Harvey, P. H. and Rudder, B. (1977). Sexual dimorphism, sociometric sex ratio and body weight in primates. *Nature* **269**, 797-800.
- Clutton-Brock, T. H., Guinness, F. E. and Albon, S. D. (1982). *Red Deer: The Behavior and Ecology of Two Sexes*. Chicago, IL: Chicago University Press.
- Crompton, R. H., Sellers, W. I. and Thorpe, S. K. S. (2010). Arboreality, terrestriality and bipedalism. *Philos. Trans. R. Soc. Lond. B* **365**, 3301-3314.
- Crowner, M. L., Peric, G., Stepic, F. and Lee, S. (2005). Assailant and victim behaviors immediately preceding inpatient assault. *Psychiatr. Q.* **76**, 243-256.
- Darwin, C. (1899). *The Expression of the Emotions in Man and Animals*. New York, NY: D. Appleton and Company.
- Enquist, M. (1985). Communication during aggressive interactions with particular reference to variation in choice of behaviors. *Anim. Behav.* **33**, 1152-1161.
- Farlow, J. O., Gatesy, S. M., Holtz, T. R., Hutchinson, J. R. and Robinson, J. M. (2000). Theropod locomotion. *Am. Zool.* **40**, 640-663.
- Furuichi, T. (1997). Agonistic interactions and matrilineal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. *Int. J. Primatol.* **18**, 855-875.
- Galdikas, B. M. F. (1985). Adult male sociality and reproductive tactics among orangutans at Tanjung Puting. *Folia Primatol.* **45**, 9-24.
- Gordon, A. D., Green, D. J. and Richmond, B. G. (2008). Strong postcranial size dimorphism in *Australopithecus afarensis*: results from two new resampling methods for multivariate data sets with missing data. *Am. J. Phys. Anthropol.* **135**, 311-328.
- Green, D. J. and Gordon, A. D. (2008). Metacarpal proportions in *Australopithecus africanus*. *J. Hum. Evol.* **54**, 705-719.
- Harcourt, A. H. (1978). Strategies of emigration and transfer by primates, with particular reference to gorillas. *Z. Tierpsychol.* **48**, 401-420.
- Hohmann, G. and Fruth, B. (2003). Intra- and intersexual aggression by bonobos in the context of mating. *Behavior* **140**, 1389-1413.
- Inouye, S. E. (1992). Ontogeny and allometry of African ape manual rays. *J. Hum. Evol.* **23**, 107-138.
- Ivancevic, V. G. (2009a). New mechanics of traumatic brain injury. *Cogn. Neurodyn.* **3**, 281-293.
- Ivancevic, V. G. (2009b). New mechanics of generic musculo-skeletal injury. *Biophys. Rev. Lett.* **4**, 273.
- Jarman, P. J. (1983). Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. *Biol. Rev. Camb. Philos. Soc.* **58**, 485-520.
- Jouffroy, F. K., Godinot, M. and Nakano, Y. (1991). Biometrical characteristics of primate hands. *Hum. Evol.* **4**, 269-306.
- Jurmain, R. (1997). Skeletal evidence of trauma in African apes with special reference to the Gombe chimpanzees. *Primates* **38**, 1-14.
- Kano, T. (1992). *The Last Ape. Pygmy Chimpanzee Behavior and Ecology*. Stanford, CA: Stanford University Press.
- Kivell, T. L., Kibii, J. M., Churchill, S. E., Schmid, P. and Berger, L. R. (2011). *Australopithecus sediba* hand demonstrates mosaic evolution of locomotor and manipulative abilities. *Science* **333**, 1411-1417.
- Legerstee, M., Corter, C. and Kienapple, K. (1990). Hand, arm, and facial actions of young infants to a social and nonsocial stimulus. *Child Dev.* **61**, 774-784.
- Lindegard, B. (1953). Variations in human bodybuild; a somatometric and X-ray cephalometric investigation on Scandinavian adults. *Acta Psychiatr. Neurol. Scand. Suppl.* **86**, 1-163.
- Lovejoy, C. O., Simpson, S. W., White, T. D., Asfaw, B. and Suwa, G. (2009). Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. *Science* **326**, e1-e8.
- Manning, J. T. and Taylor, R. P. (2001). Second to fourth digit ratio and male ability in sport: implications for sexual selection in humans. *Evol. Hum. Behav.* **22**, 61-69.
- Manning, J. T., Scutt, D., Wilson, J. and Lewis-Jones, D. I. (1998). The ratio of 2nd to 4th digit length: a predictor of sperm numbers and concentrations of testosterone, luteinizing hormone and oestrogen. *Hum. Reprod.* **13**, 3000-3004.
- Marzke, M. W. (1983). Joint functions and grips of the *Australopithecus afarensis* hand, with special reference to the region of the capitate. *J. Hum. Evol.* **12**, 197-211.
- Marzke, M. W. (1997). Precision grips, hand morphology, and tools. *Am. J. Phys. Anthropol.* **102**, 91-110.
- Marzke, M. W., Marzke, R. F., Linscheid, R. L., Smutz, P., Steinberg, B., Reece, S. and An, K. N. (1999). Chimpanzee thumb muscle cross sections, moment arms and potential torques, and comparisons with humans. *Am. J. Phys. Anthropol.* **110**, 163-178.
- Maynard Smith, J. and Price, G. R. (1973). The logic of animal conflict. *Nature* **246**, 15-18.
- McHenry, H. M. (1986). Size variation in the postcranium of *Australopithecus afarensis* and extant species of Hominoidea. *J. Hum. Evol.* **1**, 149-155.
- McHenry, H. M. (1991). Sexual dimorphism in *Australopithecus afarensis*. *J. Hum. Evol.* **20**, 21-32.
- McHenry, H. M. (1996). Sexual dimorphism in fossil hominids and its socioecological implications. In *The Archaeology of Human Ancestry: Power, Sex and Tradition* (ed. J. Steele and S. Shennan), pp. 91-109. New York, NY: Routledge.
- Midlo, C. (1934). Form of hand and foot in primates. *Am. J. Phys. Anthropol.* **19**, 337-389.
- Morris, D. (1977). *Manwatching: A Field Guide to Human Behavior*. New York, NY: H. N. Abrams.
- Napier, J. R. (1960). Studies of the hands of living primates. *Proc. Zool. Soc. Lond.* **134**, 647-657.
- Napier, J. R. (1962). The evolution of the hand. *Sci. Am.* **207**, 56-65.
- Napier, J. R. (1965). Evolution of the human hand. *Proc. R. Inst. Great Britain* **40**, 544-557.
- Neave, N., Laing, S., Fink, B. and Manning, J. T. (2003). Second to fourth digit ratio, testosterone and perceived male dominance. *Proc. Biol. Sci.* **270**, 2167-2172.
- Ogihara, N., Kunai, T. and Nakatsukasa, M. (2005). Muscle dimensions in the chimpanzee hand. *Primates* **46**, 275-280.
- Parker, G. A. (1974). Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.* **47**, 223-243.
- Parker, G. A. (1983). Arms races in evolution – an ESS to the opponent independent costs game. *J. Theor. Biol.* **101**, 619-648.
- Pickford, M., Senut, B., Gommery, D. and Treil, J. (2002). Bipedalism in *Orrorin tugenensis* revealed by its femora. *C. R. Palevol* **1**, 191-203.
- Plavcan, J. M. (1999). Mating systems, intrasexual competition and sexual dimorphism in primates. In *Comparative Primate Socioecology* (ed. P. C. Lee), pp. 241-269. Cambridge: Cambridge University Press.
- Plavcan, J. M. (2000). Inferring social behavior from sexual dimorphism in the fossil record. *J. Hum. Evol.* **39**, 327-344.
- Plavcan, J. M. (2004). Sexual selection, measurement of sexual selection, and sexual dimorphism in primates. In *Sexual Selection in Primates: New and Comparative Perspectives* (ed. P. M. Kappeler and C. P. van Schaik), pp. 230-252. Cambridge: Cambridge University Press.
- Plavcan, J. M. and van Schaik, C. P. (1997a). Intrasexual competition and body weight dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* **103**, 37-68.
- Plavcan, J. M. and van Schaik, C. P. (1997b). Interpreting hominid behavior on the basis of sexual dimorphism. *J. Hum. Evol.* **32**, 345-374.
- Price, M. E., Dunn, J., Hopkins, S. and Kang, J. (2011). Anthropometric correlates of human anger. *Evol. Hum. Behav.* **33**, 174-181.
- Putts, D. A. (2010). Beauty and the beast: mechanisms of sexual selection in humans. *Evol. Hum. Behav.* **31**, 157-175.
- Reno, P. L., McCollum, M. A., Meindl, R. S. and Lovejoy, C. O. (2010). An enlarged postcranial sample confirms *Australopithecus afarensis* dimorphism was similar to modern humans. *Philos. Trans. R. Soc. Lond. B* **365**, 3355-3363.
- Richmond, B. G. and Jungers, W. L. (2008). *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. *Science* **319**, 1662-1665.



- Rolian, C., Lieberman, D. E. and Hallgrímsson, B.** (2010). The coevolution of human hands and feet. *Evolution* **64**, 1558-1568.
- Schubert, T. W. and Koole, S. L.** (2009). The embodied self: making a fist enhances men's power-related self-conceptions. *J. Exp. Soc. Psychol.* **45**, 828-834.
- Schultz, A. H.** (1930). The skeleton of the trunk and limbs of higher primates. *Hum. Biol.* **2**, 303-438.
- Straus, W. L.** (1942). Rudimentary digits in primates. *Q. Rev. Biol.* **17**, 228-243.
- Susman, R. L.** (1979). Comparative and functional morphology of hominoid fingers. *Am. J. Phys. Anthropol.* **50**, 215-236.
- Susman, R. L.** (1988). Hand of *Paranthropus robustus* from Member 1, Swartkrans: fossil evidence for tool behavior. *Science* **240**, 781-784.
- Susman, R. L.** (1994). Fossil evidence for early hominid tool use. *Science* **265**, 1570-1573.
- Susman, R. L.** (1998). Hand function and tool behavior in early hominids. *J. Hum. Evol.* **35**, 23-46.
- Szalai, F. and Szamado, S.** (2009). Honest and cheating strategies in a simple model of aggressive communication. *Anim. Behav.* **78**, 949-959.
- Szamado, S.** (2008). How threat displays work: species-specific fighting techniques, weaponry and proximity risk. *Anim. Behav.* **76**, 1455-1463.
- Walther, F. R.** (1984). *Communication and Expression in Hoofed Mammals*. Bloomington, IN: Indiana University Press.
- Watkins, B. T., Parkinson, D. and Mensforth, R. P.** (1993). Morphological evidence for the abandonment of forelimb dominance in *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* **16**, 205.
- Watts, D. P., Muller, M., Amsler, S. J., Mbabazi, G. and Mitani, J. C.** (2006). Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *Am. J. Primatol.* **68**, 161-180.
- Wrangham, R. W.** (1999). Evolution of coalitionary killing. *Am. J. Phys. Anthropol.* **110** Suppl. **29**, 1-30.
- Wrangham, R. and Peterson, D.** (1996). *Demonic Males: Apes and the Origins of Human Violence*. Boston, MA: Houghton Mifflin.
- Young, R. W.** (2003). Evolution of the human hand: the role of throwing and clubbing. *J. Anat.* **202**, 165-174.
- Zihlman, A. L. and McFarland, R. K.** (2000). Body mass in lowland gorillas: a quantitative analysis. *Am. J. Phys. Anthropol.* **113**, 61-78.